

Familiarity and relatedness: Effects on social learning about foods by Norway rats and Mongolian gerbils

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In recent experiments in which the social influences on feeding in Mongolian gerbils were investigated, observer gerbils acquired food preferences from conspecific demonstrators only if the demonstrators and observers were either related or familiar. Even then, the effects of demonstrator gerbils on observers' food choices lasted less than 24 h. In similar experiments with Norway rats, the familiarity/relatedness of demonstrators and observers had little effect on social learning, and the demonstrators' influence on observers' food choices lasted many days. We examined the causes of these differences and found that, after observer gerbils interacted with either unfamiliar or familiar conspecific demonstrators that had been fed using procedures typically used to feed demonstrator rats, they showed long-lasting social learning about foods, whereas observer rats interacting with conspecific demonstrators that had been fed as demonstrator gerbils normally are fed showed effects of familiarity/relatedness to demonstrators on their social learning about foods. Procedural differences, rather than species differences, seem to be responsible for reported inconsistencies in social learning about foods by rats and gerbils.

The results of numerous experiments have shown that, after naive Norway rats (observer rats) interact with recently fed conspecifics (demonstrator rats), the observers exhibit a substantial enhancement of their preferences for whatever food their respective demonstrators ate (see, e.g., Galef & Wigmore, 1983; Heyes & Durlach, 1990; Posadas-Andrews & Roper, 1983; Winocur, 1990). Such socially induced food preferences in Norway rats (*Rattus norvegicus*) can last as long as several days (Galef, 1989), and they are transmitted from demonstrator rat to conspecific observer regardless of whether the two animals are related or unrelated, familiar or unfamiliar (Galef, Kennett, & Wigmore, 1984).

In a recent paper, Valsecchi and colleagues (Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996) provided evidence that, in Mongolian gerbils (*Meriones unguiculatus*),

as in Norway rats and house mice (*Mus domesticus*; Valsecchi & Galef, 1989), interaction of a demonstrator gerbil with a conspecific observer enhances the observer's preference for the food that its demonstrator ate. However, unlike observer rats (Galef et al., 1984), observer gerbils acquired flavor preferences from conspecific demonstrators only when those demonstrators were either genetically related or familiar to their observers (Valsecchi et al., 1996). Further, even when demonstrator Mongolian gerbils and their observers were from the same litter and had been raised together, the effects of the food fed to demonstrators on the food choices of their observers were relatively short-lived. Observer gerbils exhibited a preference for their respective demonstrators' diets for 16 but not for 24 h after the start of testing (Valsecchi et al., 1996).

Valsecchi et al. (1996) attributed the difference between their finding of an important impact of familiarity and relatedness on social learning in Mongolian gerbils and Galef et al.'s (1984) failure to find such an effect in Norway rats to a difference between Norway rats and Mongolian gerbils in the relative likelihood that members of each species will behave aggressively when they first meet conspecifics that are both unfamiliar and unrelated. Unfamiliar/unrelated Mongolian gerbils fight when they meet for the first time, whereas the young female Norway rats that have served as subjects in most experiments on social learning about foods are far less likely to behave aggressively on first encounter.

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Consistent with the view that anxiety induced by meeting a strange conspecific interferes with social learning about foods in gerbils is recent evidence showing that observer Mongolian gerbils treated with an anxiolytic agent (benzodiazepine chlordiazepoxide) before they interact with an unfamiliar/unrelated conspecific demonstrator learn food preferences from those demonstrators as readily as they learn food preferences from familiar/related demonstrators (Choleris et al., 1998). It is, however, also possible that procedural differences in studies of social learning in the two species contribute significantly to observed differences between Norway rats and Mongolian gerbils in the parameters of their social learning about foods.

The most obvious difference in how studies on social learning have been conducted when gerbils (Valsecchi et al., 1996) rather than rats (Galef & Wigmore, 1983) have been used as subjects lies in the ways in which demonstrators of each species are fed before they interact with conspecific observers. Rat demonstrators are typically placed on a 23-h schedule of food deprivation for several days and are then fed a flavored diet for 1 h immediately before they interact with their observers. This procedure ensures that each demonstrator eats its day's rations immediately before it interacts with an observer.

Because it is difficult to induce Mongolian gerbils to eat unfamiliar powdered foods on a 23-h schedule of food deprivation (Choleris & Valsecchi, unpublished observation), gerbil demonstrators are typically food deprived for 16 h and then given access to a flavored powdered food for 8 h before they interact with their respective observers (Valsecchi et al., 1996). When fed in this way, demonstrator gerbils eat only 20% of their days' rations in the last 2 h of the 8-h feeding period (Choleris & Valsecchi, unpublished observation). As a result of this difference in the way in which Norway rat and Mongolian gerbil demonstrators are fed before interacting with observers, there is likely to be a difference in the strength of the diet-identifying olfactory signals (Galef & Stein, 1985) emitted by demonstrator rats and by demonstrator gerbils when the members of each species interact with conspecific observers.

Procedures typically used to feed demonstrator Norway rats, like those typically used to feed demonstrator Mongolian gerbils, produce analogues of events that might be expected to occur in nature. A foraging rodent of any species may eat either a small or a large amount of food immediately or some time before it interacts with a conspecific. However, it seems likely that a rodent that ate a small amount of food long before interacting with a conspecific observer would have less influence on its observer than would a rodent that ate large amounts of food immediately before interacting with its observer. Consequently, differences in the results of studies of social influences on food choice obtained with Mongolian gerbils and Norway rats might be due not only to differences in their likelihood of behaving aggressively toward unfamiliar/unrelated conspecifics (or to other differences

between Norway rats and Mongolian gerbils) but also to differences in the time elapsing between when demonstrators eat substantial amounts of food and when they interact with their observers (Galef & Kennett, 1985).

We undertook the experiments reported here in order to determine whether differences in experimental procedures can account for observed differences in the robustness of social learning of food preferences in Norway rats and Mongolian gerbils.

EXPERIMENT 1

We employed procedures typically used to feed Norway rat demonstrators to look for differences between Mongolian gerbils and Norway rats in effects of familiarity and relatedness on the social transmission of food preferences. To control, at least in part, for differences between rats and gerbils in aggression, we used as subjects highly aggressive unfamiliar/unrelated and nonaggressive familiar/related adult male Norway rats rather than the young females that have served as subjects in most previous experiments with rats.

Method

Subjects: Mongolian gerbils. Fourteen adult (3-month-old) Mongolian gerbils, obtained from Tumblebrook Farm (Brookfield, MA), and 38 adult (3- to 10-month-old) Mongolian gerbils, selected from a colony maintained in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario), served as subjects. Members of the McMaster colony were descendants of breeding stock purchased 2 years earlier from Tumblebrook Farm. Each gerbil was assigned to a pair constituted of 2 animals of the same sex and age (± 1 month).

We used brothers or sisters from the McMaster colony that we had housed together from birth as members of familiar/related pairs ($n = 12$). One member of each unfamiliar/unrelated pair ($n = 14$) came from the McMaster colony, and the other directly from Tumblebrook Farm. Members of unfamiliar/unrelated pairs never interacted before the start of the experiment and were known to have no grandparent in common.

Subjects: Norway rats. Twenty-seven pairs of adult (3- to 4-month-old), male Long-Evans rats, obtained either directly from Charles River Canada (St. Constant, Quebec) or from a colony maintained in the vivarium of the McMaster University Psychology Department, served as subjects. Members of the McMaster colony were descendants of breeding stock acquired 2 years earlier from Charles River Canada.

We used brothers from the McMaster colony that had been housed together from birth as members of familiar/related pairs ($n = 12$); members of unfamiliar/unrelated pairs ($n = 15$) consisted of one animal from the McMaster vivarium and one obtained directly from Charles River Canada. Members of unfamiliar/unrelated pairs never interacted before the start of the experiment and were known to have no great grandparent in common.

Diets. We composed two flavored diets by adding either 20 g of Hershey's Cocoa (Diet Coc) or 10 g of McCormick's Pure Ground Cinnamon (Diet Cin) to 1,000 g of powdered Purina Rodent Laboratory Diet 5001 (Diet Pur).

Apparatus: Mongolian gerbils. During the 4 days of the experiment, we housed members of each familiar/related demonstrator-observer pair of gerbils on opposite sides of a 1.25-cm screen partition that divided a $42.5 \times 24 \times 27$ cm, wire-mesh hanging cage into two $21.5 \times 24 \times 27$ cm compartments. For the same 4-day pe-

riod, we housed members of unfamiliar/unrelated demonstrator–observer pairs of gerbils in individual $20 \times 24 \times 27.5$ cm wire-mesh hanging cages.

At the beginning of the final day of the experiment, demonstrator and observer gerbils interacted across a 1.25-cm screen partition while in a cage identical to that in which we housed familiar/related demonstrator–observer pairs, except that we (1) removed the cage in which each demonstrator–observer pair interacted from the rack that normally held it, (2) placed a clear Plexiglas lid (measuring 42.5×27 cm) on the cage to prevent subjects from escaping from it, and (3) placed the cage directly on a tray containing wood chip bedding. We videotaped each demonstrator–observer pair of gerbils in the test cage while they interacted.

Because gerbils often spill powdered food, we offered powdered diet to them in feeding devices that we constructed by fixing an 8.0×4.0 cm petri dish in the center of a 10.0×5.0 cm petri dish. We placed the powdered food in the smaller petri dish so that almost all spilled food was trapped in the space between the dishes. Any additional spillage was easily collected in paper trays that we placed directly beneath each feeding device, under the hanging cage in which we maintained each observer.

Apparatus: Norway rats. We housed the members of each familiar/related pair of Norway rats on opposite sides of a 1.25-cm screen partition in a wire-mesh hanging cage divided into two equal compartments, exactly as we had housed members of familiar/related pairs of gerbils. We housed members of each unfamiliar/unrelated pair of rats as we housed members of familiar/related pairs of rats, except that we placed the two members of each unfamiliar pair in separate cages rather than across a screen partition from one another in the same cage.

We presented powdered food to rats in semicircular stainless steel cups measuring 10 cm in diameter and 5 cm deep that we filled to only half their depth to prevent spillage.

Procedure. The procedures that we used with gerbils and rats were identical, except as noted in Steps 1 and 3 below.

Step 1. Because of the difficulty in getting gerbils (but not rats) to begin feeding on powdered food, for 48 h before the start of the experiment, we placed a cup containing powdered Diet Pur in the home cages of both demonstrator and observer gerbils, along with the pelleted Diet Pur that was their normal maintenance diet.

Step 2. To begin the experiment, we moved all the subjects to their wire-mesh cages (as described in the Apparatus section), placed demonstrators on a 23-h schedule of food deprivation, and provided observers with pellets of Diet Pur ad lib.

Each day, for 2 successive days, we offered the demonstrators, while in their home cages, Diet Pur for 1 h each day. Following a third 23-h period of deprivation, we offered half of the demonstrators a weighed sample of Diet Cin, while in their respective home cages. At the same time, we offered the other half of the demonstrators a weighed sample of Diet Coc. While feeding the demonstrators, we also removed food pellets from the cages of all the observers.

Step 3. When rats were the subjects, as soon as the demonstrators had finished their 1-h meal of flavored food, we moved each demonstrator rat to the opposite side of the screen partition from an observer rat in that observer's home cage and allowed demonstrator and observer to interact through the partition for 15 min. Thus, each demonstrator and observer pair of Norway rats assigned to the familiar/related condition interacted in their respective home cage, whereas demonstrator and observer Norway rats assigned to the unfamiliar/unrelated condition interacted in the home cages of the observer members of each pair.

When gerbils were the subjects, we moved both demonstrator and observer from their respective home cages to opposite sides of the partition in the test apparatus, in which we videotaped them while they interacted for 15 min.

Step 4. After each demonstrator and observer had interacted for 15 min, we (1) removed all demonstrators from the experiment,

(2) moved observer gerbils back to the hanging cages from which we had taken them, and (3) offered each gerbil and rat observer a choice between weighed samples of Diet Cin and Diet Coc for 24 h.

Step 5. Twenty-four hours after we introduced weighed food cups into the cage containing each observer, we removed the food cups, reweighed them, and calculated the percentage of each observer's total food intake during the 24-h choice test that was Diet Cin.

Step 6. An experimenter unaware of the familiarity/relatedness of pairs of gerbils scored videotapes of their interactions.

Results and Discussion

The main results of Experiment 1 are presented in Figures 1A and 1B, which show, respectively, the amount of Diet Cin eaten by observer rats and observer gerbils during the 24-h choice test. As is clear from inspection of the two histograms, after 24 h, both observer rats (Figure 1A) and observer gerbils (Figure 1B) whose demonstrators ate Diet Cin ate more Diet Cin during the test period than did observer rats and gerbils whose demonstrators ate Diet Coc. As can also be seen in Figure 1, effects of diets fed to the demonstrators on the diet choices of their observers were clearly present whether demonstrators and observers were Norway rats or Mongolian gerbils and whether they were members of familiar/related or unfamiliar/unrelated demonstrator–observer pairs.

For both rats and gerbils, two-way analyses of variance (ANOVAs) performed on the percentage of Diet Cin eaten by observers during the 24-h choice test revealed a significant main effect of flavor of the food fed to demonstrators on the food choices of their observers [gerbils, $F(1,20) = 14.90, p < .001$; rats, $F(1,25) = 22.06, p < .001$], no significant effect of familiarity/relatedness [gerbils, $F(1,20) = 1.22, n.s.$; rats, $F(1,25) = 0.18, n.s.$], and no significant interaction between main effects [gerbils, $F(1,20) = 0.49, n.s.$; rats, $F(1,25) = 0.06, n.s.$].

Student's *t* tests revealed that, for both familiar/related and unfamiliar/unrelated rats [familiar, $t(12) = 2.75, p < .01$; unfamiliar, $t(13) = 2.87, p < .01$] and familiar/related and unfamiliar/unrelated gerbils [familiar, $t(10) = 2.79, p < .01$; unfamiliar, $t(12) = 2.83, p < .01$], there was a significant effect of demonstrators' diet on the food choices of their observers.

Scoring of videotapes revealed that members of unfamiliar/unrelated pairs of gerbils spent significantly more time interacting through the partition that separated them than did familiar/related pairs of gerbils [Student's *t* test, $t(22) = 5.98, p < .001$] when *interaction* was defined as two animals simultaneously facing the screen partition with their noses less than 2.5 cm apart. We found no significant correlation between the time spent interacting by members of a pair of gerbils and the percentage of whichever diet the demonstrator in that pair ate that its observer ate [Spearman rank-order correlation, $r(25) = .14, n.s.$].

Two findings are of particular interest: (1) over a 24-h period, observer gerbils exhibited robust preferences for the foods that their respective demonstrators ate irrespective of whether their demonstrators were familiar and related or unfamiliar and unrelated; and (2) potentially aggressive, unfamiliar/unrelated, adult male rats showed

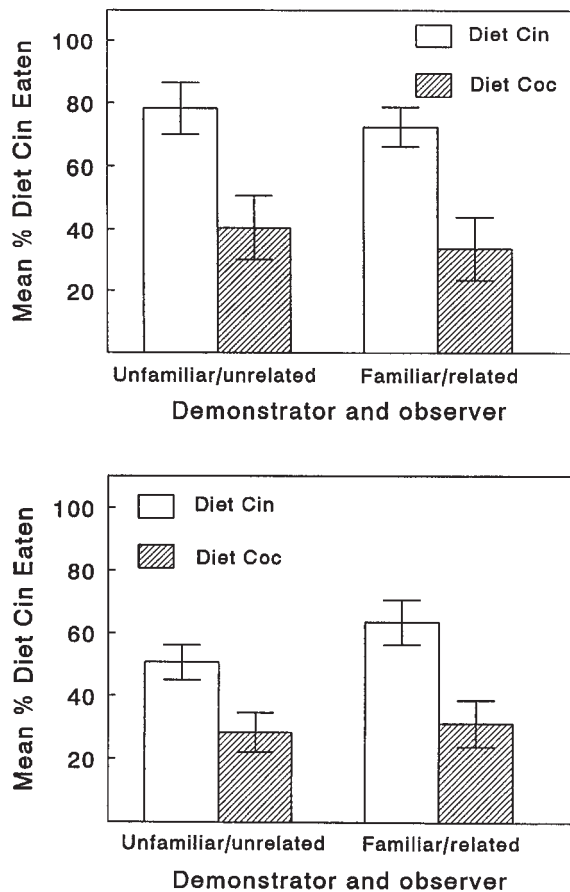


Figure 1. Mean amount of Diet Cin eaten as a percentage of total amount ingested during a 24-h choice test by observer rats (upper panel) or gerbils (lower panel), as a function of the diet fed to their conspecific demonstrators. Flags = ± 1 SEM.

social learning of food preferences as large as did nonaggressive familiar/related adult male rats.

Taken together, the results of Experiment 1 showed that, using the feeding procedure that is typically used with Norway rats, both unfamiliar/unrelated male rats and unfamiliar/unrelated gerbils showed socially induced food preferences lasting at least 24 h, despite the fact that both unfamiliar/unrelated gerbils and unfamiliar/unrelated adult male rats are normally highly aggressive toward one another when they first meet. Thus, in neither rats nor gerbils was the potential for aggressive interaction between demonstrator and observer an impediment to social learning about foods when demonstrators ate large amounts shortly before they interacted with their respective observers.

EXPERIMENT 2

In Experiment 2, we directly compared the size of socially induced food preferences in Norway rats when we employed procedures typically used to feed demonstrators in studies of gerbils (Valsecchi et al., 1996) with procedures typically used to feed demonstrators in stud-

ies of Norway rats (Galef & Wigmore, 1983). Our goal was to determine whether differences in the results of previous studies in which rats and gerbils were used as subjects could be explained by procedural differences alone.

Method

Subjects. Twelve 7-week-old and twenty-four 6-week-old, female Long-Evans rats purchased from Charles River Canada (St. Constant, Quebec), as well as twelve 6-week-old, female Long-Evans rats purchased from Harlan Sprague-Dawley, Inc. (Indianapolis, IN), served as subjects. By using animals from different suppliers as demonstrators and observers in each repetition of the experiment, we could be sure that the members of each demonstrator–observer pair were unrelated to and unfamiliar with one another. In successive weeks, the rats acquired from Harlan Sprague-Dawley served first as observers, then as demonstrators, whereas 12 of the animals from Charles River Canada served first as observers, then as demonstrators. The remainder of the rats from Charles River Canada served only as observers.

Data were lost from 3 pairs of rats when a demonstrator failed to eat more than 5 g before interacting with its observer ($n = 1$) or an observer failed to eat more than 10 g during the 23-h test period ($n = 2$). When demonstrators eat less than 5 g of Diet before interacting with their observers, they might not produce diet-identifying olfactory cues strong enough to be identified by their observers. Observers failing to eat 10 g of powdered food during a 24-h test, have usually suffered a problem with their water supply and are therefore not truly comparable to demonstrators that had ad-lib access to both food and water during the test period.

Apparatus and Diets. We housed each subject in an individual wire-mesh hanging cage measuring $20 \times 24 \times 27.5$ cm. We used the same food cups as those we used with rats in Experiment 1, as well as the same diets as those we had used in Experiment 1.

Procedure. The procedure we used to feed the 12 pairs of subjects whose demonstrators were fed as Norway rat demonstrators typically are (referred to below as the 1-h feeding procedure) was the same as that we used to feed demonstrator rats in Experiment 1. In brief, we (1) placed each demonstrator rat on a 23-h schedule of food deprivation for 3 days, (2) let each demonstrator feed for 1 h on either Diet Cin or Diet Coc on the 3rd day of scheduled feeding, (3) then placed each demonstrator in the cage of an observer and let demonstrator and observer interact for 30 min, and (4) offered each observer, for 23 h, a choice between weighed samples of Diet Cin and Diet Coc.

The sole differences between the treatment of rats in the present condition and that for those serving as subjects in Experiment 1 was in the sex, age, and origins of subjects, in the amount of time that demonstrators and their observers interacted (30 min rather than 15 min), and in whether demonstrator and observer were separated by a screen partition while they interacted.

We treated the remaining 12 demonstrator–observer pairs exactly as we treated those assigned to the 1-h feeding procedure, except that we fed the demonstrator in each pair as Mongolian gerbils are typically fed in experiments on social learning about food (referred to below as the 8-h feeding procedure). In brief, we (1) deprived demonstrator rats of food for 16 h, (2) fed the demonstrators either Diet Cin or Diet Coc for 8 h, (3) placed each demonstrator in the cage of an observer, (4) let demonstrator and observer interact freely for 30 min, and (5) offered each observer a choice between weighed samples of Diet Cin and Diet Coc for 23 h.

Results and Discussion

The main results of Experiment 2 are presented in Figure 2, which shows the amount of Diet Cin eaten during the 23-h test period by observer rats that interacted with

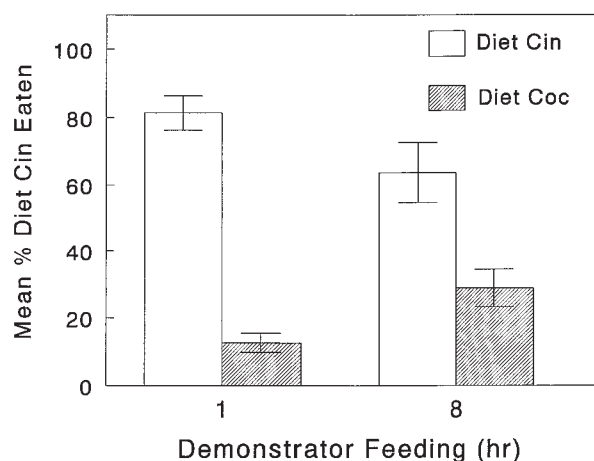


Figure 2. Mean amount of Diet Cin eaten as a percentage of total amount ingested during a 23-h choice test by observer Norway rats that were unfamiliar with and unrelated to their respective conspecific demonstrators and interacted with demonstrators that had been fed using either the 1-h or the 8-h feeding procedure. Flags = ± 1 SEM.

demonstrator rats given food for either 8 h or 1 h before interacting with their respective observers. As can be seen from Figure 2, observers exposed to demonstrators that were fed by either method showed a significant impact of the food fed to their demonstrators on their own food choices [1-h feeding: Student's t test, $t(19) = 10.94$, $p < .0001$; 8-h feeding: $t(22) = 3.28$, $p < .01$]. There was, however, a significant interaction between the method used to feed demonstrators and diet; observers that interacted with demonstrators that had been fed either Diet Cin or Diet Coc for 1 h showed a significantly larger impact of the diet fed to their respective demonstrators on their own food choices than did observers that interacted with demonstrators that had been fed for 8 h before we placed them with their respective observers [$F(1,41) = 7.03$, $p < .02$]. The 1-h feeding method resulted in significantly stronger social influence on food choices by rats than did the 8-h feeding method.

We speculate that this difference in the magnitude of social influence on food choice is the result of demonstrator rats that were fed for 1 h having eaten more food close to the time when they interacted with their observers than had demonstrator rats that were fed for 8-h. The fact that, after 24 h of testing, demonstrator Norway rats in the present experiment that we fed for 8 h had a significant effect on the food choices of their unfamiliar/unrelated conspecific observers, whereas demonstrator Mongolian gerbils that were fed for 8 h did not have a similar effect on the food choices of their unfamiliar/unrelated conspecific observers (Valsecchi et al., 1996), could be due either to a difference in the aggressiveness of adult gerbils and immature rats, as the data of Choleris et al. (1998) suggest, or to some other difference between rats and gerbils.

EXPERIMENT 3

In Experiment 3, we directly compared socially induced food preferences in Mongolian gerbils when demonstrators were fed for either 1 or 8 h. As in Experiment 2, our goal was to determine whether differences in the strength of social learning previously reported in Mongolian gerbils and Norway rats could be explained, at least in part, by procedural differences.

Method

Subjects. Thirty-four male and 38 female 3-month-old, experimentally naive Mongolian gerbils served as observers. An additional 34 males and 38 females served as demonstrators. Each demonstrator and each observer was assigned to a same-sex pair whose members had never interacted and had no great grandparent in common.

All the subjects were born and reared in the vivarium of the Dipartimento di Biologia Evolutiva e Funzionale of the University of Parma to stock acquired from Tumblebrook Farms (Brookfield, MA).

Apparatus. Demonstrators and observers were individually housed in Plexiglas cages measuring $25 \times 38 \times 15$ cm that we provided with spill-proof feeders (Valsecchi, Mainardi, Sgolfo, & Taticchi, 1989). Interactions between demonstrators and observers took place in a Plexiglas cage measuring $27 \times 24 \times 14$ cm that was divided diagonally into two equal triangular areas by a screen partition.

Diets. We made cinnamon- and cocoa-flavored diets by mixing, respectively, either 10 g of powdered cinnamon (Diet Cin) or 20 g of cocoa (Diet Coc) with 1,000 g of powdered Mil Morini Rodent Chow (Diet Mil; Morini, Reggio Emilia, Italy). In previous studies, we had found Diet Cin and Diet Coc to be roughly equipalatable to gerbils (Valsecchi et al., 1996).

Procedure. We treated the demonstrator and observer gerbils that we assigned to the 1-h feeding condition exactly as we had treated the Mongolian gerbils in Experiment 1, except that we induced demonstrators to eat on schedule by giving them a 1-h exposure to Diet Mil when 16 h food deprived before the start of the experiment, rather than by giving them ad-lib access for 24 h to unflavored powdered diet before the start of the experiment.

We treated the gerbils assigned to the 8-h feeding condition exactly as we treated the demonstrators assigned to the 1-h feeding condition, except that we food deprived the demonstrators assigned to the 8-h feeding group for 16 h and then fed them either Diet Cin or Diet Coc for 8 h before allowing them to interact with their respective observers.

Results and Discussion

The main results of Experiment 3 are presented in Figure 3, which shows the amount of Diet Cin eaten, as a percentage of total amount ingested during the 24-h choice test, by observer gerbils whose demonstrators ate either Diet Cin or Diet Coc for either 1 or 8 h before interacting with their respective observers. A 2×2 ANOVA performed on arcsine-transformed percentage scores revealed a significant main effect of diet fed to demonstrators on their respective observers' food choices during the 24-h choice test [$F(1,68) = 9.08$, $p < .005$] but no significant effect of duration of demonstrator feeding [$F(1,68) = 0.16$, n.s.] and no significant interaction between main effects [$F(1,68) = 0.75$, n.s.].

We found a statistically significant effect of the diet fed to the demonstrators assigned to the 1-h feeding con-

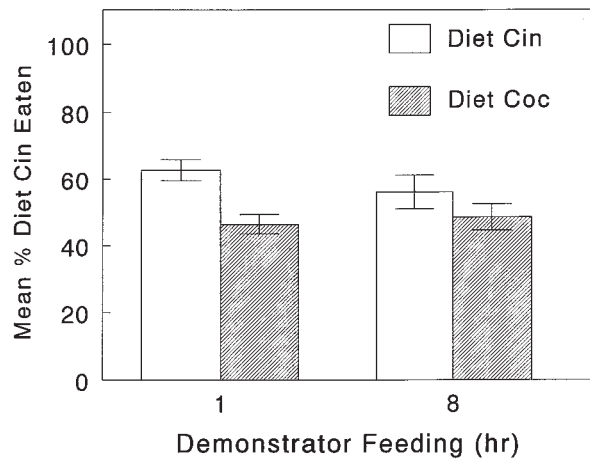


Figure 3. Mean amount of Diet Cin eaten as a percentage of total amount ingested during a 24-h choice test by observer gerbils that were unfamiliar with and unrelated to their respective conspecific demonstrators and interacted with demonstrators that had been fed using either the 1-h or the 8-h feeding procedure. Flags = ± 1 SEM.

dition on the food choices of their observers [Student's t test, $t(33) = 3.71$, $p < .001$] but no comparable effect of the diet fed to the demonstrators assigned to the 8-h feeding condition on the food choices of their respective observers [$t(35) = 1.18$, n.s.].

The results of Experiment 3 are consistent with the outcome (1) of Experiment 1 in the present series, where demonstrator gerbils that were fed for 1 h before they interacted with unfamiliar/unrelated conspecific observers significantly influenced the food choices of their observers for 24 h and (2) of previous experiments by Valsecchi and co-workers (Valsecchi et al., 1996) showing that demonstrator gerbils fed for 8 h before interacting with observers did not significantly affect their observers' subsequent food choices over a 24-h period.

GENERAL DISCUSSION

In Experiment 1 of the present series, demonstrator Mongolian gerbils fed for 1 h influenced the food choices of their observers for at least 24 h, regardless of whether those observers and their demonstrators were familiar and related or unfamiliar and unrelated. These results contrast with those of Valsecchi et al. (1996), who allowed demonstrators to feed for 8 h before interacting with their observers and found (1) relatively brief social effects on food preferences, even in familiar/related pairs of demonstrator and observer gerbils, and (2) a large effect of relatedness and familiarity of gerbil subjects on susceptibility to social influence on their food choices.

We suggest, on the basis of these outcomes, that (1) demonstrators fed for only 1 h before they interact with observers have a greater probability of emitting effective diet-identifying cues while interacting with their observers than do demonstrators fed for 8 h before inter-

acting with their observers and (2) the effects of familiarity and relatedness on social induction of food preference are seen only when experimental conditions produce a relatively low probability of social induction of a food preference.

The results of Experiments 2 and 3 of the present series are consistent with such an interpretation. In both experiments, socially induced preferences produced both in unrelated/unfamiliar Norway rats and in unrelated/unfamiliar Mongolian gerbils by demonstrators fed for 8 h were significantly smaller than were those induced in unfamiliar/unrelated rats and gerbils by demonstrators fed for 1 h.

Combining the results of Experiment 1 with those of Experiments 2 and 3, it is apparent that effects on the social transmission of food preference of familiarity and relatedness are observable in a 24-h test only when demonstrators are fed for 8 h and, we suggest, only when the diet-identifying cues emitted by demonstrators are, consequently, relatively weak. The familiarity and relatedness of members of demonstrator-observer pairs and the consequent probability of aggression between pair members interacts with the feeding regime of demonstrators and the consequent strength of diet-identifying signals emitted by demonstrators to determine both the magnitude and the duration of social influences on food choice in rodents.

Although the present experiments were not designed to examine directly differences in the susceptibility of Mongolian gerbils and Norway rats to social influence on food choice, our results do suggest that rats may be more susceptible to such influence than are gerbils. In both Experiments 1 and 3, the apparent amount of social influence on food choice in gerbils was somewhat less than one normally sees in rats, and, in Experiment 2, demonstrator rats fed for 8 h still exerted substantial influence on the food choices of their observers over a 24-h period, whereas, in both the present (Experiment 3) and past experiments (Valsecchi et al., 1996), demonstrators fed for 8 h did not influence their observers' food choices over 24 h.

However, methods used with both rats and gerbils were arrived at over the years because they maximized the effects of social learning on food choice in Norway rats. In Timberlake's (1990) terminology, the apparatus, diets, and procedures we used had been "tuned" to maximize the reliability of social learning about foods by rats. Obviously, details of procedure that maximize social learning in Norway rats may not be optimal for demonstrating parallel effects in Mongolian gerbils. Consequently, apparent species differences may reflect matches and mismatches between subject species and procedures rather than biologically interesting differences in behavior (see Timberlake, 1990, pp. 36-38, for further discussion).

Not enough is known of the ecology or foraging behavior of Norway rats and Mongolian gerbils living in natural circumstances to be able to deduce in which species attention to socially acquired information about foods is likely to provide greater benefits (Boyd & Richerson, 1988). Considerable additional work in both laboratory

and field would be needed to be confident of comparisons between species in the strength of social influence on food choice.

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